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BY

W. J. REES, D.Sc.

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SYNOPSIS

The Atlantic species of the larval octopod genus *Macrotritopus* (*M. equivocus*, *M. scorpio*, *M. kempi* and *M. danae*), together with some *Macrotritopus*-like larvae described by Degner (1925), have been re-examined, and the type material of all but the first two species has been available for study. All these forms were found to be growth stages of *Scaeurgus unicirrhus* (Delle Chiaje), an octopus of the continental shelf. The *Macrotritopus* larvae appear to be able to delay settlement if they are swept over very deep water by water movements, and to continue growing to nearly twice the normal size for metamorphosis. These large larvae (found also in other groups of animals) are now termed extended pelagic stages, and their significance in dispersal and in maintaining the homogeneity of populations of widely distributed species is discussed.

CONTENTS

A. INTRODUCTION

This study originated from a desire to carry further earlier work on the planktonic stages of *Octopus vulgaris* (Rees, 1950, 1952). In particular, it was hoped that late planktonic stages of this species could be obtained from a search of plankton hauls made in the tropical Atlantic by the ships of the "Discovery" Investigations. During the course of this work a number of *Macrotritopus* larvae were collected, and it was the remarkable similarity of the youngest *Macrotritopus* larvae to those of *Octopus vulgaris* (except in the very long third arms) which led me to re-examine them in relation to a known adult or adults.

The startling agreement of the chromatophore patterns in *Macrotritopus* and *Octopus vulgaris* suggested some relationship, but further investigations showed conclusively the *Macrotritopus* could not be linked with any littoral species. Final conclusions indicate that all the so-called *Macrotritopus* spp. of the Atlantic belong to one species, and that the adult is *Scaeurgus unicirrhus* (Delle Chiaje), a benthic octopod living at moderate depths near the edge of the continental shelf.

B. THE GENUS *Macrotritopus*

Grimpe (1922) proposed the name *Macrotritopus* as a generic name for a juvenile pelagic octopod, *Octopus gracilis* Verrill, because the third arms greatly exceeded the others in length. Later, Robson (1929*b*, p. 168, *et seq.*) changed Verrill's name to *equivocus* because the name *gracilis* was preoccupied. While recognizing that *Macrotritopus* was only a convenient label for juveniles, whose adult stages might or might not be known, he referred four other forms to it, viz.:

Octopus scorpio (Berry), *Macrotritopus kempi* Robson, *Octopus bandensis* Hoyle and *Octopus elegans* Brock. Of these, *Octopus* (*Macrotritopus*) *equivocus* Robson and the first three above were described from the Atlantic and the Mediterranean. The last two are Indo-Pacific species and need not concern us further here. Later, Joubin & Robson (1929) described *Macrotritopus danae* from the collections of the Danish Dana Expeditions. All the known Atlantic specimens of *Macrotritopus* are juveniles exhibiting no sings of hectocotylization.

It has also been found necessary to reconsider some larvae described by Degner (1925) as *Scaeurgus* (Troschel sp. juv.), because on re-examination they prove to be *Macrotritopus* larvae.

The *Macrotritopus* forms which have been described are so distinctive in appearance that their true identity is masked by larval characteristics. In this connection the views of earlier workers are of interest. Verrill (1884), in considering his own *Octopus gracilis* (i.e., *equivoca*), was "very certain it is not the young of any known species." Robson (1929*b*) was unable to make up his mind about the status of these forms, as is evident from his statement: "We must either conclude that they are the young forms of species hitherto undescribed or that they undergo some kind of metamorphosis in the course of subsequent development, as a result of which they assume the adult form of some described species." More recently, Pickford (1945) in discussing the American forms *M. equivoca* and *M. scorpio*, expressed the opinion that "There is no possibility that these strikingly distinct young animals with their very long third arms could belong to a *vulgaris*-like species." The same author (1947) added " whatever they may be they are clearly not the young of any littoral species." Voss (1951) considered the possibility of *M. scorpio* being the larval form of *Scaeurgus* but had insufficient material to reach any decision.

These views reflect the need for clearing up the status of the Atlantic forms of *Macrotritopus*, and except for *M. equivoca* I have been privileged to re-examine all the original material reported on by Degner (1925), Robson (1929), Joubin & Robson (1929) and Voss (1951) together with many additional specimens from the plankton catches of the " Discovery " Investigations, 1925–1939. I have been able to do this through the generosity of Dr. Anton Brunn (for the loan of Dana specimens) ; Dr. Gilbert Voss (for the use of two specimens of *Macrotritopus* from Florida) ; and Dr. N. A. Mackintosh and Dr. Helen Bargmann, for "Discovery" material. I also wish to thank Dr. G. R. de Beer, F.R.S., and Dr. H. W. Parker for valuable suggestions, Mr. G. L. Wilkins for his superb drawings (Pl. 3 and figures 1-6), and Mr. H. O. Ricketts for his great care in examining large samples of plankton for octopod larvae.

(a) ***Octopus (Macrotritopus) equivocus* Robson**

Octopus gracilis Verrill 1884, p. 236 *non* Eydoux & Souleyet 1852, p. 13.
Macrotritopus equivocus Robson 1929*a*, p. 311.
Octopus (*Macrotritopus*) *equivocus*, Robson, 1929*b*, p. 169.
Octopus (*Macrotritopus*) *equivoca*, Joubin & Robson 1929, p. 93.

TYPE LOCALITY. "Albatross" St. 2084, 40° 16′ 50″ N., 65° 05′ 15″ W., south of Cape Sable, Nova Scotia, 1,290 fms. ; 1 specimen.

TABLE I

Measurements in mm.

Length of body (? ventral mantle length)	11·0
Mantle width	7·0
Interocular width	6·5
Length of head and body	17·0
Arm length :	
1st	19·0
2nd	21·0
3rd	42·0
4th (damaged)	—

Verrill thought that the specimen was a juvenile of a species growing to a large size and was convinced that it was not the young of any known species. He noted the extraordinarily long third arms, the second arms being only half their length. On the evidence available from the description, it agrees with other *Macrotritopus* larvae noted later in having (in alcohol) large purplish chromatophores on the body and the head. There are also purplish spots (i.e., chromatophores) in front of and behind each sucker, this feature being common to all *Macrotritopus* and to many other octopod larvae.

Verrill notes that the first 3–5 suckers on the lower pairs of arms are uniserial and that this arrangement is not found on the dorsal arms. This is unusual, but a minor point, as the arrangement may be due to unequal contraction of the arms during fixation.

Three features about this larva are noteworthy. It is the largest known specimen of *Macrotritopus*; it was caught over deep water and its occurrence (off Nova Scotia) is well to the north of any other records of larvae of this genus.

(b) ***Octopus (Macrotritopus) scorpio*** (Berry)

Polypus scorpio Berry 1920, p. 299, pl. 16, fig. 4.
Octopus (*Macrotritopus*) *scorpio*, Robson 1929*b*, p. 169.
Octopus (*Macrotritopus*) *scorpio*, Joubin & Robson, 1929, p. 93.

LOCALITY. "Bache" St. 10204, off Biscayne Bay, Florida; 20.iii.1914; 75–0 m.; 1 specimen.

Berry gives total length as 22 mm., and 4·5 mm. as dorsal mantle length. The measurements given below have been calculated from his figure in order to provide some basis for comparison with other larvae.[1]

TABLE II

Measurements in mm.

Ventral mantle length	4·73
Dorsal mantle length	5·89
Mantle width	3·85
Interocular width	3·8
Arm length:	
1st	3·1
2nd	7·27
3rd	14·0
4th	4·62
Mantle-arm index	31·8

Berry had some doubts about his species being specifically distinct from Verrill's *gracilis*, but mentioned the inequality in the length of the first and second arms, the still greater length of the third arms and the minute papillations as distinguishing features. The chromatophore pattern is only briefly mentioned.

(c) ***Octopus (Macrotritopus) kempi*** Robson.

Macrotritopus kempi Robson, 1929*a*, p. 311.
Octopus (*Macrotritopus*) *kempi*, Robson, 1929*b*, p. 170.

TYPE LOCALITY. "Discovery" St. 276, 5° 54′ S., 11° 19′ E., off the mouth of the Congo; 5.viii.1927; N 70B, 110–0 metres; 2 syntypes (B.M. 1947.3.12.1–2).

Robson regarded this species as a very distinct one on account of its narrow head,

[1] Berry's figure is not very satisfactory; the head is said to be "distinctly narrower than the body," but as pointed out by Robson it is nearly as wide as the body in the figure; Berry's "dorsal mantle length" of 4.5 mm. is probably the distance from the apex to the nuchal ridge, and the measurement given in the table is the distance between the apex and the point midway between the eyes.

wide mantle, the smooth surface of the skin, the size of the web and the distinctive colour pattern. He also drew attention to the proportions of the third arm, and mentioned that there were 11–12 filaments in each demibranch.

Robson (1929*b*, p. 171) drew attention to the position where this species was found over deep water and about 10 miles off the edge of the continental shelf. This species is further discussed and the specimens re-described on pp. 76–77.

(d) *Octopus (Macrotritopus) danae* Joubin & Robson

Octopus (*Macrotritopus*) *danae*, Joubin & Robson, 1929, p. 87, fig. 1.
Octopus (*Macrotritopus*) *danae*, Joubin 1937, p. 33, fig. 33.

Type locality. "Dana" St. 1152, 30° 17′ N., 20° 44′ W., 23.ix.21 (160 metres). Paratypes from the Western Mediterranean, off Guiana and off W. Cuba.

Joubin and Robson were clearly puzzled about the relationship of their species with previously described forms. However, they created a new species chiefly on the grounds that although the third arms were very long (74–80% of the total length), the second arms were also particularly well developed ; the third arm exceeding the second by 1·7–2·1 times its length. Other differences were mentioned.

The measurements given by Joubin & Robson are given below for seven specimens examined by them.

Table III

Measurements in mm.

	No. of specimen.													
	2		1		3		4		5		6		7	
Mantle length (? dorsal) . .	13		13·5		10		10·5		10		9		12	
Arms :	Left	Right	L.	R.	L.	R.	L.	R.	L.	R.	L.	R.	L.	R.
1st	20	21	16	16	12	14	13	14	13	14	10	—	13	12
	28	32	25	25	22	20	22	21	22	23	17	18	21	19
	48	37	38	36	37	42	37	33	35	35	28	32	39	36
	27	29	20	—	18	18	18	19	17	19	15	12	19	17
Indices :														
Mantle width, percentage length .	57		48		60		57		55		61		—	
Head width, percentage length .	46		44		50		52		50		55		50	
3rd arms, percentage total length .	78		74		80		78		77		78		76	
3rd arm > 2nd arm . .	1·7 times		1·5		2·1		1·6		1·5		1·7		1·8	

The above figures have not been used in my investigations, and all the specimens which I have been able to see have been measured again as it was desirable to get additional readings.

The " Dana " material forwarded to me, together with paratypes in the British Museum (Natural History), contains a few specimens apparently not seen by Joubin & Robson, so it has been deemed desirable to examine this material in detail in the next section.

(e) ***Scaeurgus*** (Troschel sp. juv.) Degner, 1925

" Thor " St. 184 : 38° 10′ N., 22° 23′ E., Gulf of Corinth ; 17.viii.1910 ; 65 metres of wire.

Some octopod larvae from the Mediterranean in which the third arms were particularly well developed and long were described by Degner (1925, p. 79) ; these are essentially *Macrotritopus*-like forms which have to be considered in any discussion of the *Macrotritopus* problem. Degner assigned these larvae to *Scaeurgus* because one of his specimens was showing the beginning of a hectocotylus on the third left arm. A sinistral hectocotylus is a characteristic of *Scaeurgus* and also of *Pteroctopus tetracirrus*, another Mediterranean species ; the latter species was not discussed by Degner in relation to his larvae.

The relationship of these forms to other described species of *Macrotritopus* has not been fully realized by earlier workers, and it is possible that they have been misled by Degner's fig. 52, which portrays a larva quite unlike the usual *Macrotritopus*. It has been possible to re-examine these larvae in this investigation (see p. 74).

C. A RE-EXAMINATION OF *Macrotritopus* LARVAE

All the material of these larvae which it has been possible to gather together has been re-examined. It includes the type material of *Macrotritopus danae*, *M. kempi*, Degner's *Scaeurgus*, two new specimens from Florida (the type locality of *M. scorpio*), as well as some additional specimens brought to light from an examination of hauls made in the tropical Atlantic by the "Discovery" Expeditions (1925–1939).

(a) ***Macrotritopus danae*** Joubin & Robson

Larvae have been available from the following stations of the Danish " Dana " Expeditions 1920–22 (see Schmidt, 1929) :

St. 1123^{vii}, 37° 48′ N., 2° 44′ E., Western Mediterranean, 26.ix.21, S. 200, 200 metres of wire ; 1 specimen (8·25 mm. in ventral mantle length).

St. 1124^{ii}, 37° 15′ N., 2° 55′ E., Western Mediterranean 27.ix.21, S. 200, 200 metres of wire ; 2 specimens (2·5, 6·75 and 9·0 mm. in ventral mantle length); also Joubin & Robson's No. 2 specimen.

St. 1174^{iii}, 5° 35′ N., 51° 08′ W., off Guiana, 16.xi.1921, S. 200, 300 metres of wire ; 1 specimen (now dry).

St. 1223^{iv}, 22° 06′ N., 84° 58′ W., off Cuba, 1.ii.22, S. 200, 50 metres of wire ; 1 specimen (4·95 mm. in ventral mantle length).

New measurements have been made on the six larvae at my disposal.

No. 1. This specimen, in sea-water formalin, is now rather faded with faint traces of chromatophores only on the third arms. The interbrachial web is moderately developed ; its depth in the A sector is about 3·0 mm., and about the same in other sectors (except sector E, where it is distinctly less well developed).

No. 2 is a young and very interesting larva in which the third arm is more than twice the length of the other arms ; the latter and the interbrachial web are but little developed. These shorter arms have the thin whip-like tips so characteristic also

TABLE IV.—*Macrotritopus danae*

Measurements in mm.

	No. 1	2	3	4	5	6
Ventral mantle length	8·25	2·5	6·75	9·0	9·75	4·95
Dorsal mantle length	10·8	3·0	11·55	13·35	12·0	5·7
Mantle width	7·05	2·4	6·0	7·35	7·8	3·6
Interocular width	6·45	2·55	4·8	6·75	6·0	4·2
Diameter of eye	2·55	0·9	2·25	2·4	2·55	1·35
Arm length						
1st arm	14·25	1·5	8·7	14·25	15·75	3·0
2nd arm	22·5	1·75	15·45	23·25	27·0	4·95
3rd arm	37·5	4·25	27·75	32·25	33·0	12·75
4th arm	18·0	1·75	11·25	21·0	21·0	4·05
Diameter largest sucker :						
Diam. sucker, 1st arm	0·5–0·55	0·25	0·3	0·5	0·5	0·2
,, ,, 2nd arm	0·55–0·6	0·25	0·4	0·6	0·55	—
,, ,, 3rd arm	0·75–0·8	0·25	0·6	0·75	0·8	0·45
Indices :						
Mantle arm index	22·0	58·8	24·35	27·9	29·6	38·8
Sucker index, 3rd	9·7	10	8·9	8·34	8·21	9·1
,, ,, 2nd	7·28	10	5·95	6·67	5·64	—
,, ,, 1st	6·67	10	4·44	5·56	5·13	4·04

of early stages of *Octopus vulgaris*, and their undeveloped state is reflected in the number of suckers they carry. From the base of the arm there are 3–4 uniserial suckers, 1–2 pairs of biserial suckers followed by rudiments of others. The third arm, however, has about 7–8 well-formed, biserial suckers and rudiments of others towards the tip. All the chromatophores have disappeared.

No. 3. In this specimen the right eye is torn and protruding (allowance has been made for this in measurements) and the third left arm is mutilated. Except for traces of two rows on the outer surface of the third arms the chromatophores have disappeared.

No. 4. The mantle-shape in this specimen is as figured by Joubin & Robson. The interbrachial web is moderately developed, the deepest sector being D. The chromatophore pattern has all but disappeared and there is no trace left on the mantle. On the dorsal head there are two in the position indicated for *M. scorpio* by Berry but the others are very faint. On the third arms there are traces of a few, opposite suckers, and two faintly indicated rows on the outer surface of these arms.

No. 5. This paratype (B.M. 1929.6.29.1.) has retained far more of its colour than any of the other "Dana" larvae ; this is perhaps partly due to the fact that the specimen is in alcohol, and partly also because it has been kept for the greater part of the time in total darkness. However, all chromatophores of the mantle have disappeared except three in a row along the *dorsal* mantle edge and the deep-seated ones of the visceral mass. Those of the dorsal side of the head can be counted and conform to the *vulgaris* pattern.

The chromatophores of the third arms are contracted. On the outer surface there is, proximally, a single row, followed distally by a double row. Here and there there is a suggestion of the pattern seen in *M. kempi*.

No. 6. No trace remains of the original chromatophore pattern.

(b) *Macrotritopus kempi* and other "Discovery" larvae

In addition to the syntypes of *M. kempi*, larvae have been found at the following stations of the "Discovery" Expeditions (1925–1939):

St. 276, 5° 54′ S., 11° 19′ E., N.W. of mouth of the Congo, 5.viii.1927, TYF, 150(–0) m.; 2 specimens of 3·3 and 4·5 mm. in ventral mantle length.

St. 276, N. 100 B, 110–0 m.; 2 syntypes of *M. kempi* Robson and 1 specimen of 3·75 mm. in ventral mantle length.

St. 290, 3° 25′ 25″ N., 16° 50′ 52″ W., off West Africa. 24.viii.1927, N 100 B, 86–0 m.; sounding 5,165 m.; 1 specimen of 5·4 mm. in ventral mantle length.

St. 1592, 09° 31′ N., 17° 37′ W., off West Africa, 17.x.1935, TYFB, 200–0 m.; 1 specimen of 6·0 mm. ventral mantle length.

St. 1594, 04° 15′ N., 12° 58′ W., off West Africa, 19.x.1935, TYFB, 144–0 m.; 1 specimen of 6·15 mm. in ventral mantle length.

St. 2646, 05° 38′ N., 14° 03′ W., off West Africa, 19.iv.1939, TYFB, 250–0 m.; 1 specimen of 3·2 mm. in ventral mantle length.

St. 2646, TYFB, 1,500–800 m.; 1 specimen of 3·45 mm. in ventral mantle length.

The standard measurements of the Discovery specimens are given in Table V.

TABLE V.

Measurements in mm.

	No.									
	7	8	9	10	11	12	13	14	15	16
Ventral mantle length	8·1	7·65	3·3	4·5	3·75	5·4	6·00	6·15	3·2	3·45
Dorsal mantle length	9·6	9·75	3·75	6·45	4·95	7·05	6·75	9·0	3·9	4·2
Mantle width	9·75	7·8	3·6	3·9	3·75	4·05	4·95	5·85	2·55	—
Interocular width	6·0	5·4	3·3	4·5	3·45	3·75	4·65	5·7	2·70	3·0
Diameter of eye	—	—	—	—	—	—	—	—	1·0	—
Arm length:										
1st	13·5	11·25	2·25	4·2	2·25	5·4	5·25	7·8	1·5	2·40
2nd	22·2	18·0	3·75	6·75	2·70	8·25	8·25	15·0	1·65	3·0
3rd	32·25	—	10·95	16·5	10·5	16·0	15·3	28·5	6·0	6·75
4th	18·45	14·25	2·25	4·5	2·85	6·5	8·25	10·05	1·5	2·25
Diameter, largest suckers:										
2nd arm	0·45	0·35	0·2	0·25	0·2	0·2	0·3	0·4	—	—
3rd arm	0·55	0·5	0·35	0·4	0·35	0·45	0·55	0·55	0·3	0·3
Indices:										
Mantle-arm index	25·15	—	30·15	27·25	33·5	33·75	39·25	21·6	55·0	51·0
Sucker index:										
3rd arm	6·8	6·54	10·6	8·88	9·34	8·33	9·17	8·95	9·1	8·7
2nd arm	5·56	4·58	6·06	5·55	5·33	3·42	5·0	6·5	6·82	—

Nos. 7 and 8 and the holotype and paratype of Robson's *M. kempi*, while Nos. 9, 10 and 11 are also from the same station.

The type is in very good condition, and so is the paratype except that in it both third arms are damaged (the left one was regenerating a new tip). Robson's figure (1929*b*, p. 170, fig. 60) gives a very good impression of the arrangements of chromatophores on the arms and head. On the ventral surface of the mantle, funnel and head the pattern of chromatophores is very like that in *O. vulgaris*. A notable feature in this specimen is the development of the other arms (1, 2 and 4), and the degree of development of the conspicuous chromatophores on them as on the third arm.

On re-examination the head is seen to be rather contracted and the mantle fully inflated in both specimens.

As regards measurements, in the species *M. kempi* the interocular width is very much less than the mantle width—a feature of considerable importance to Robson in defining his species. These specimens were picked out on board and transferred to alcohol with consequent shrinkage of the head region ; this is evident from comparison with other specimens from the same station which were not picked out of the plankton samples (Pl. 3, figs. 1 and 2). After making due allowances for size (and refraining from comment at this point on the relative proportions of the arms) all the specimens from this station undoubtedly form growth stages of one species. The most constant and characteristic feature is the chromatophore pattern of the third arms. On these (and on the second arms only to a lesser degree) the double row of chromatophores on the outer surface is exceptionally clear and distinct, especially the dorsal row. In this row each chromatophore is lengthened at right angles to the axis of the arm, giving the arm the appearance of being banded. On the sides of the third arm there is often a chromatophore at the base of each sucker but sometimes this is placed between the suckers. On the ventral face of the third arm there are also chromatophores between the bases of the suckers.

(c) ***Scaeurgus*** (Troschel sp. juv.) Degner, 1925

A re-examination of the original larvae lent by the Zoologiske Museum, København, reveals little resemblance between the published figure (Degner, 1925, p. 79, fig. 52) and the eight specimens available for study. In brief, the larvae are very similar in general appearance to other *Macrotritopus* which have been described from the Mediterranean and the Altantic (Text-figs. 1–5). Table VI gives the measurements obtained in 1952.

Degner's specimen No. 2 (specimen H above) is the largest example in this series. It has a ventral mantle length of 6·0 mm. (given as 6·3 mm. by Degner ; the differences between his measurements and mine are probably due to shrinkage in alcohol). Measurements of this and the other specimens from St. 184 are given in Table VI.

It will be seen (Text-fig. 5) that in this late larva and in the younger ones the shape and proportions of the head and mantle are quite unlike Degner's fig. 52, and have the usual form of *Macrotritopus*.

TABLE VI

Measurements in mm.

	A	B	C	D*	E	F	G*	H
Overall length (i.e., including 3rd arm)	10·5	10·95	14·85	10·95	8·55	8·7	9·6	—
Ventral mantle length	3·3	3·9	4·0	3·6	2·7	2·85	3·15	6·0
Dorsal mantle length	4·65	4·85	5·55	4·8	3·9	4·05	3·9	7·05
Mantle width	3·15	2·85	3·9	3·3	2·7	3·0	2·55	4·5
Head width	3·3	2·85	3·3	3·0	2·55	2·4	2·4	3·9
Diameter of eye	1·05	1·3	1·5	1·35	0·85	0·75	1·5	1·65
Arms:								
1st	1·8	2·1	2·55	2·25	2·0	1·25	2·0	4·65
2nd	2·4	2·85	3·15	2·7	2·5	1·75	2·3	6·75
3rd	6·75	5·55	7·95	5·1	3·75	4·0	5·25	15·0
4th	1·8	2·1	3·0	2·55	1·8	1·75	2·0	6·0
Diameter proximal (basal) sucker	0·2	0·2	0·225	—	0·2	0·2	0·18	0·3
Diameter last uniserial sucker	0·25	0·25	0·25	—	0·2	0·2	0·2	0·3
Diameter 1st biserial sucker	0·25	0·25	0·25	—	0·2	0·2	0·2	0·35
Diameter largest sucker (3rd arm)	0·3	0·25	0·3	0·3	0·22	0·22	0·25	0·45

* Specimens D and G are distorted, so that the mantle length for these is estimated.

The chromatophore pattern is rather faded but some features can be distinguished; those of the dorsal mantle have disappeared, but on the ventral surface there are about 20, scattered over the surface as in *O. vulgaris* larvae of similar size (i.e., in mantle length). Deep-seated chromatophores are present on the dorsal head as in the pattern typical of *O. vulgaris*. On the arms the chromatophores occur in a single row up to the edge of the web and then become double.

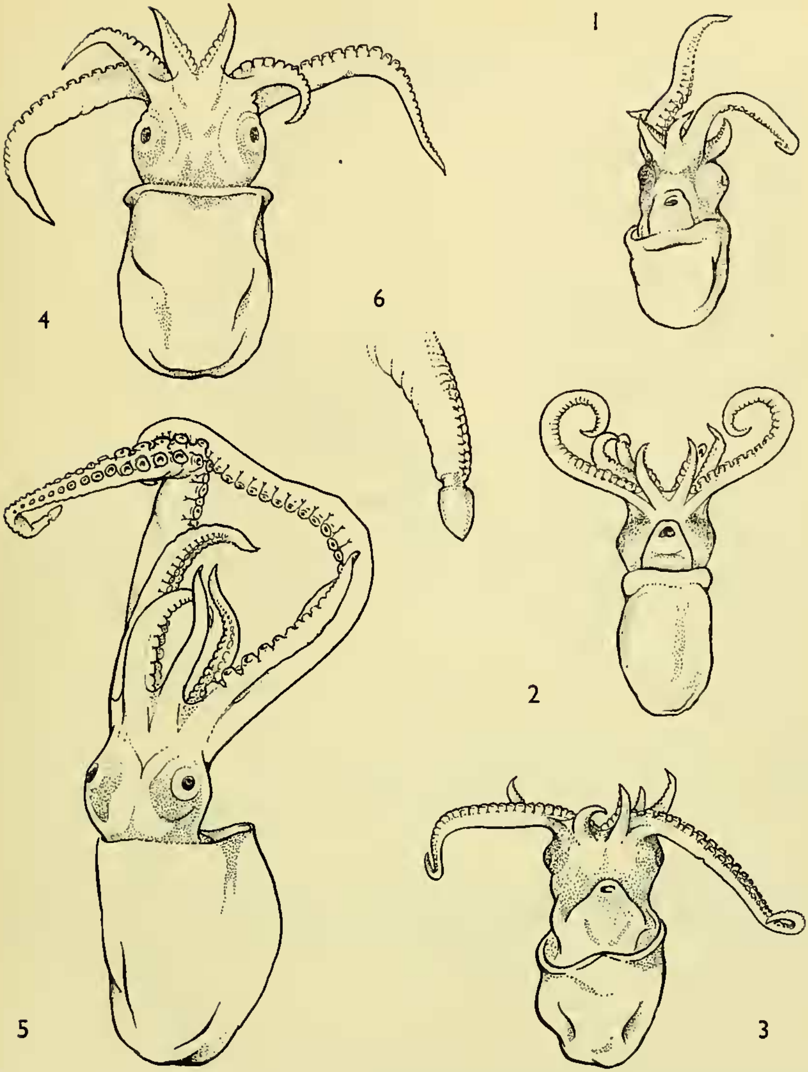
The web is fairly well developed and is of the order D = C > B > A = E. On the first arm it reaches to almost half its length. The body and arms are covered with the remains of *Köllikersche buschel* and some papillae, scattered over the mantle are developing. There are 11 gill filaments in the outer demibranch of the left gill.

The feature of greatest interest is the third left arm, which, according to Degner, was beginning to exhibit hectocotylization. I can make out no details in the structure of the tip of this arm, which is constricted off to form an egg-shaped structure with a slightly-pointed tip; its size is 0·30 mm. × 0·20 mm. (Text-fig. 6).

The identity of these larvae with *Scaeurgus* or *Pteroctopus* depends on our interpretation of this structure. Is it due to the vagaries of preservation, or can we interpret its symmetrical shape and delicately rounded appearances as a developing hectocotylus? Consideration of this feature in relation to distribution is deferred to p. 96.

(d) SPECIMENS FROM FLORIDA

Recently G. L. Voss (1951) has mentioned some *Macrotritopus* larvae which he considered to be the *scorpio* form described by Berry (1920, p. 299). By courtesy



FIGS. 1–4. *Scaeurgus* sp. Degner, 1925 : the smaller larvae from "Thor" St. 184, Gulf of Corinth ; all approximately × 6.

FIG. 5. *Scaeurgus* sp. Degner 1925: the largest larva from "Thor" St. 184 (specimen H), exhibiting signs of hectocotylization ; × 6.

FIG. 6. *Scaeurgus* sp. Degner : tip of the third left arm from specimen H with rudimentary hectocotylus ; greatly enlarged.

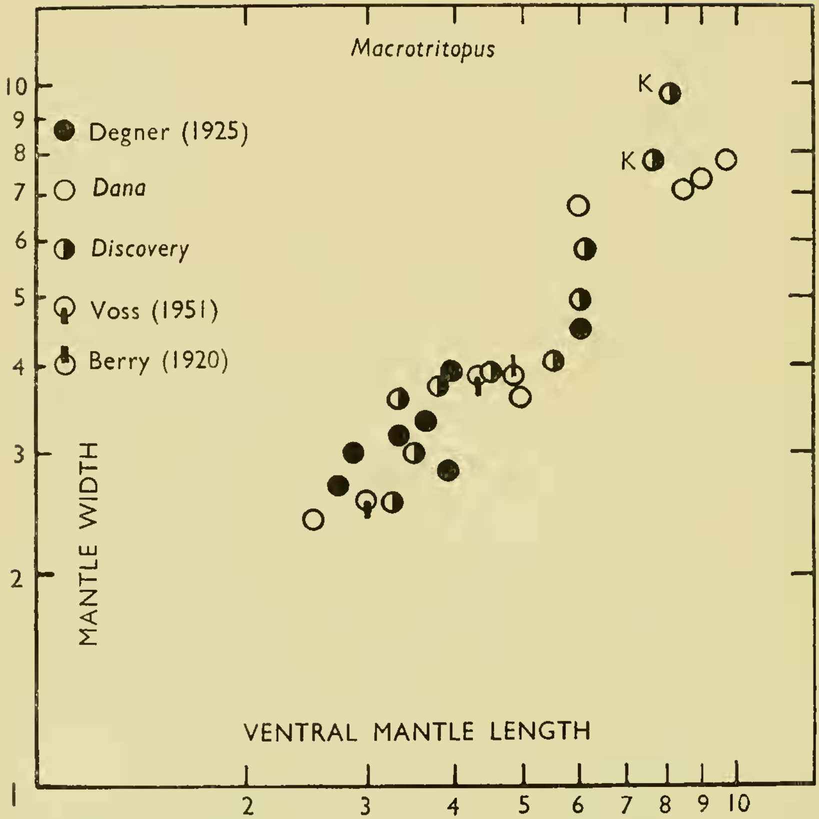


FIG. 7. Relationship between mantle width and ventral mantle length in *Macrotritopus danae*, *M. kempi*, *M. scorpio*, *Scaeurgus* sp. Degner and in additional specimens from the "Discovery" Expeditions (1925–1929). The letter *k* denotes the type material of *M. kempi*. All measurements in figs. 7–17 are in millimetres.

of Mr. Voss I have been able to examine two of the larval forms he mentions; one is in formalin and the other (No. 18) in alcohol.

I was unable to see much pattern on the surface of these larvae as their pigment has largely disappeared, presumably through exposure to sunlight after fixation. However, such pattern as remained indicated that there was nothing unusual about it, and that it was probably no different in this respect from other *Macrotritopus* larvae I had seen.

TABLE VII.—Macrotritopus *larvae from Florida*

Measurements in mm.

	No. 17	No. 18
Ventral mantle length	4·35	3·0
Dorsal mantle length	4·8	3·3
Mantle width	3·9	2·55
Interocular width	3·75	2·5
Arms:		
1st	3·15	1·3
2nd	4·95	1·5
3rd	10·2	6·0
4th	3·0	1·5
Diameter, basal sucker	0·2	0·125
,, second uniserial sucker	0·25	0·15
,, first biserial sucker	0·25	0·2
,, largest sucker, 3rd arm	1·2	0·3

D. A COMPARISON OF THE SPECIES

It was recognized quite early in the investigation that some or all of the Mediterranean-Atlantic species of *Macrotritopus* might prove to belong to one or two species, and the problem was to distinguish between growth stages and specific differences. Accordingly some characters which might reveal significant points of difference were examined.

Here it may be convenient to mention that *ventral* mantle length is used throughout in all calculations involving mantle length. It appears more reliable than the usually accepted dorsal mantle length (mid-point between the eyes to the apex of the mantle), because retraction of the head in the larva can make as big differences in measurements as distortion of the mantle margin. In the larva, too, there is a distinct ridge on the dorsal mantle which provides a useful check if by chance the ventral mantle edge is distorted.

All the accompanying graphs (except Text-figs. 9 and 10) are plotted on Wrightman's double logarithmic paper to demonstrate the relationships of the various parts. In using the data from this assorted collection of octopus larvae I have been very conscious of the inadequacy of the material, and for this reason statistical methods have not been exploited. It is, however, surprising in view of the assortment of material how well grouped the measurements are in relation to straight lines.

It became obvious early in the investigation that material in alcohol, notably Degner's *Scaeurgus* and Robson's two syntypes of *Macrotritopus kempi*, were much shrunk, the shrinkage affecting different parts unequally. With age, too, shrinkage progresses, and it must be remembered that the "Thor" collections were made 40–50 years ago and those of the "Discovery" between 1925 and 1939. Similarly the material of *M. danae* and larvae from the "Discovery" collections, although both are in formalin, are not strictly comparable from a preservation point of view, the former being flaccid (and possibly a little swollen ?) by comparison with the latter,

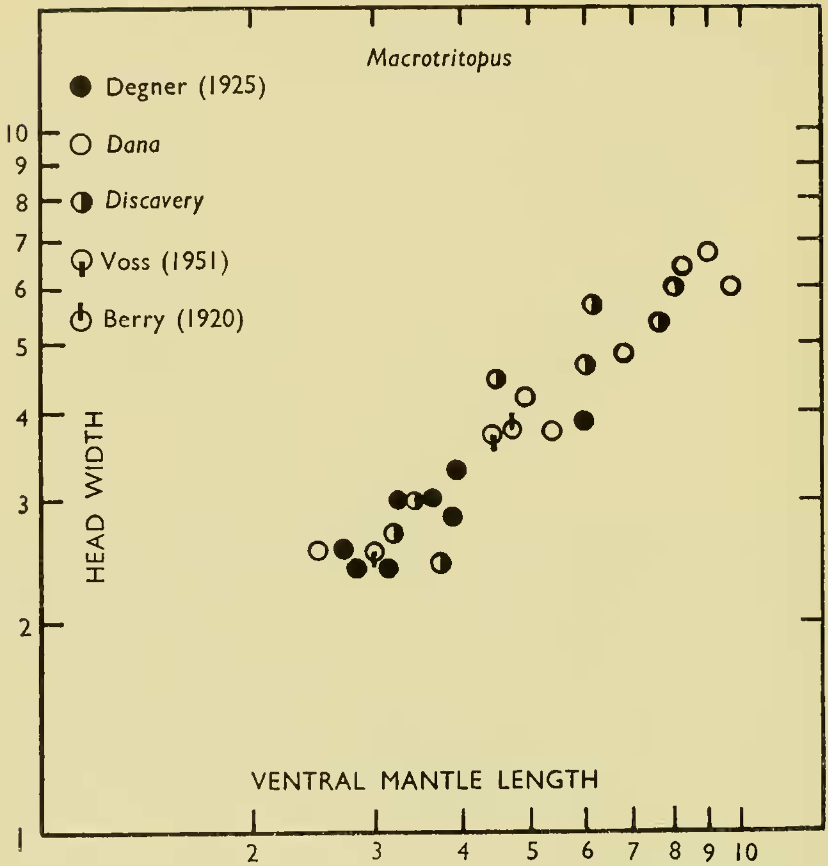


FIG. 8. Relationship between head width and ventral mantle length in *Macrotritopus danae, M. kempi M. scorpio, Scaeurgus* sp. Degner and in additional specimens from the "Discovery" Expeditions (1925–1929).

which are in fine condition. Widely different results can be obtained even with the same medium from slight differences in the method of fixation, particularly in soft-bodied animals without any substantial skeletal structures. The octopus arms in particular are highly contractile, and it is by no means improbable that in their extended condition they were two and even three times the length recorded after preservation.

(a) MANTLE LENGTH. At sizes below 4 mm. in ventral mantle length there is very little difference between the length and the width of the sac.[1] Above this size

[1] Mantle width, head width and sucker diameter grow in direct proportion to the length of the mantle Text-figs. 7, 8 and 15).

the mantle becomes distinctly elongated, except in the syntypes of *M. kempi*, where it is decidedly inflated, giving an erroneous impression of mantle proportions (Text-fig. 7, *k*). On the basis that all the specimens are growth stages, there are no significant differences in the mantle proportions of the different species, although the rather irregular plotting indicates that mantle width is not a useful diagnostic character. This is to be expected, because the mantle sac is a highly muscular pumping organ subject to alternate contraction and expansion.

(b) Head width. There are no features about head-width to suggest any significant differences between the species (Text-fig. 8).

(c) The arms. The extraordinary length of the third arm in relation to arms 1 and 2 is very striking in all the small and medium-sized larvae (Plate 3, figs. 3 and 4), but in the large ones the second arm may be 80% of the length of the third arm. Earlier workers, notably Berry (1920) and Joubin & Robson (1929), were greatly concerned with the relative proportions of these three pairs of arms, and although they had some suspicions that discrepancies in relative arm lengths might be accounted for by growth, nevertheless created species largely on these differences.

No one would deny that Degner's larvae belong to one species, although they range from 2·7–6·0 mm. in ventral mantle length. By plotting the measurements of the arms in relation to ventral mantle length in a simple graph we get the results shown in Text-fig. 9; this clearly indicates that differences in arm lengths may be accounted for by growth. A similar impression is gained from plotting the measurements for "Dana" and "Discovery" specimens in the same way (Text-fig. 10).

In the youngest known stages (2·5–3·0 mm. in ventral mantle length) the arms are already differentiated in length with the third arms greatly exceeding the second pair, which in turn are a little longer than the first pair. Between 3·0 and 4·0 mm. the difference in length between the first and second arms becomes more marked, and beyond this all three arms (1, 2 and 3) are growing rapidly.

These simple graphs suggest that the changes in relative proportions of the arms may indicate stages in allometric growth. In Text-figs. 11–13 the arm-lengths (arms 1, 2 and 3) are plotted according to the species or source of the material and for each we get a reasonable plotting, which again suggests that they all belong to one species, and it can be said that in all three arms growth is proportional to the mantle growth.

When the results for the three pairs of arms are grouped, the resulting graph demonstrates that all three grow at approximately the same rate (Text-fig. 14). The rate of growth is indicated by the slope of the mean, and it will be seen that the growth rate is the same in arms 1 and 3, but arm 2 may be growing at a slightly faster rate than the other two. The differences in arm length are dependent on when growth begins; in arm 3 it begins at a ventral mantle length of about 1·4 mm., that is, at hatching size if we assume that the larva comes from a typical octopus egg. The second arm does not begin to grow until the larva has a ventral mantle length of about 2·3 mm.; it is closely followed by the first arm when the ventral mantle length reaches 2·5 mm.

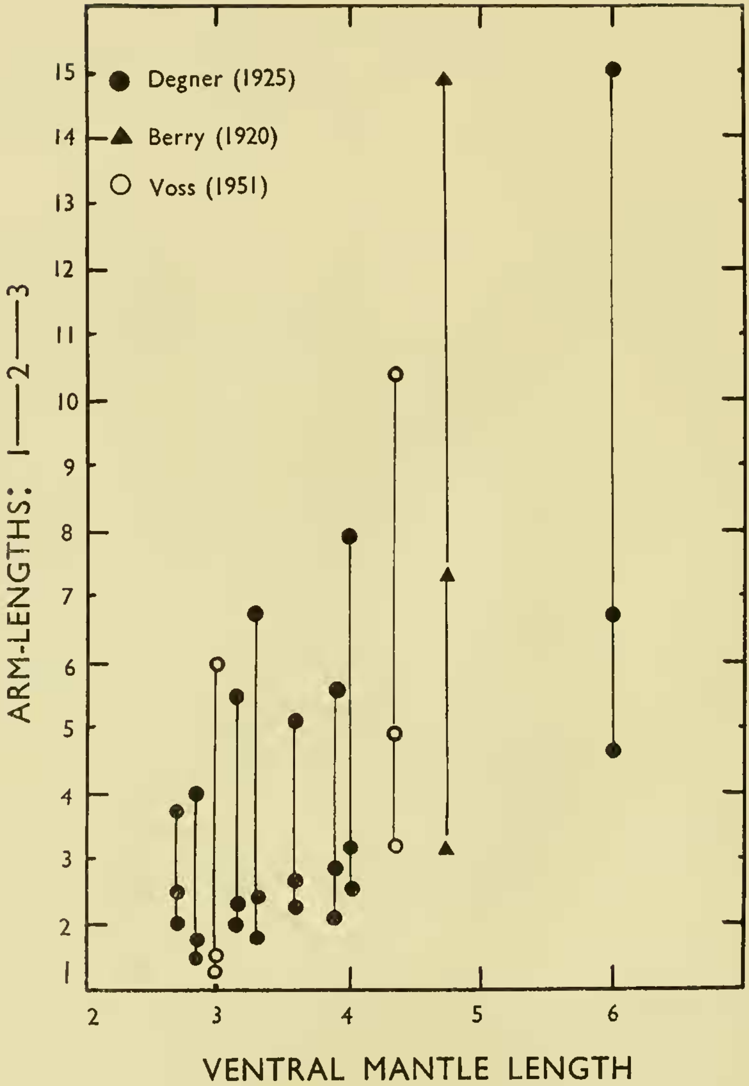


FIG. 9. Length of arms 1, 2 and 3 in relation to ventral mantle length in *Scaeurgus* sp. Degner (filled circles) and *Macrotritopus scorpio* Berry (open circles and triangles), plotted on ordinary graph paper.

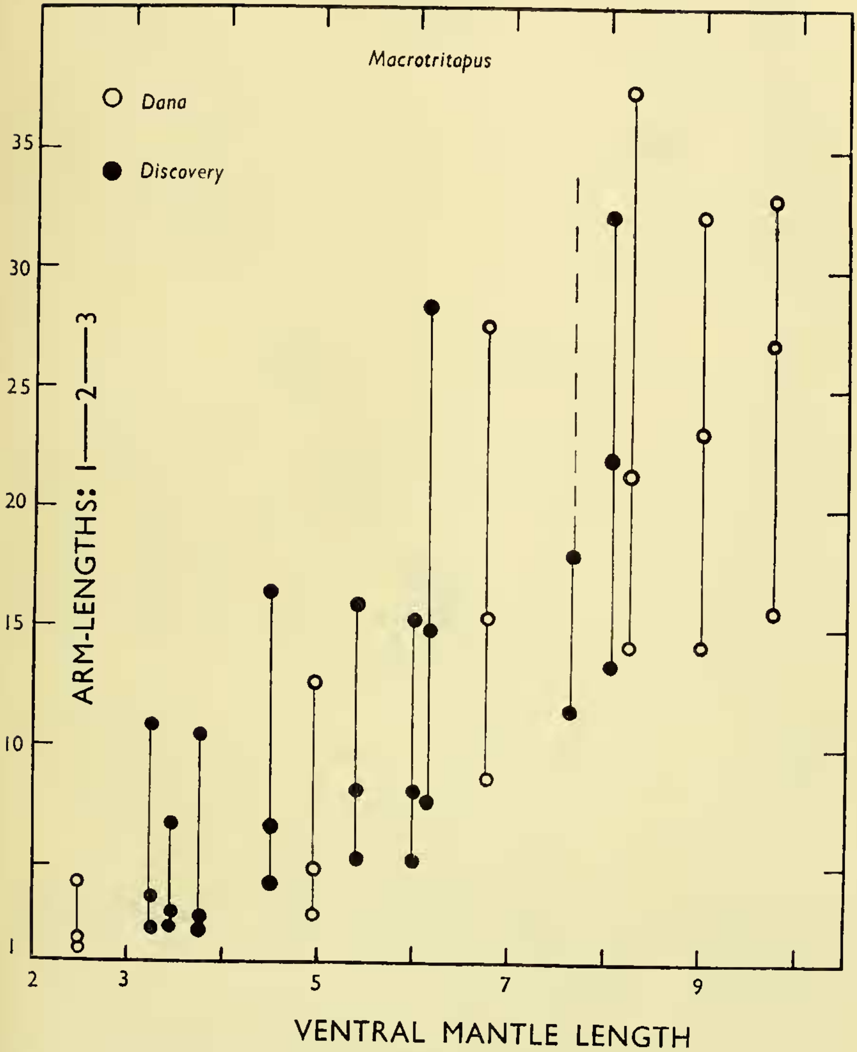


FIG. 10. Length of arms 1, 2 and 3 in relation to ventral mantle length in material from the Danish " Dana " Expeditions 1921–1922 (open circles) and from the " Discovery " Expeditions, 1925–1939 (filled circles), plotted on ordinary graph paper.

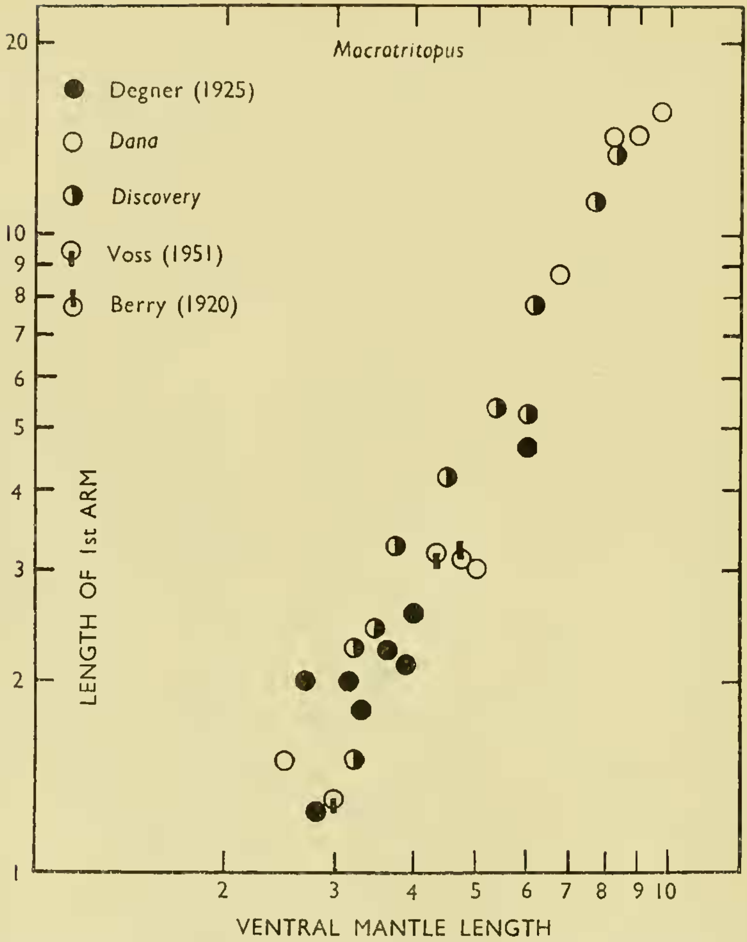


Fig. 11. Relationship of the length of the first pair of arms to ventral mantle length in *Macrotritopus danae*, *M. kempi*, *M. scorpio*, *Scaeurgus* sp. Degner, and in additional specimens from the "Discovery" Expeditions (1925–1939).

(d) Sucker diameter. The diameter of suckers of the third arm have been plotted in relation to ventral mantle length (Text-fig. 15); this graph shows more clearly than the others the shrinkage caused by storage in alcohol compared with formalin preservation. Most of the *Scaeurgus* larvae and the syntypes of *Macrotritopus kempi* (marked *k*) fall well below the line. Apart from this the graph reveals no significant differences between the species.

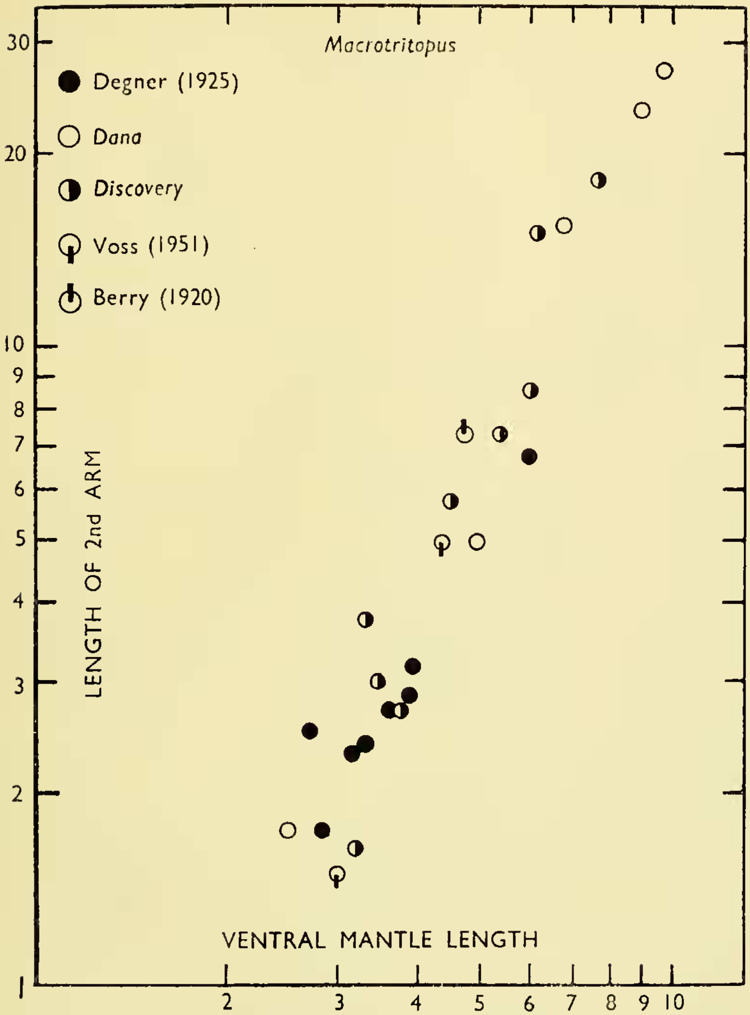


FIG. 12. Relationship of the second pair of arms to ventral mantle length in *Macrotritopus danae*, *M. kempi*, *M. scorpio*, *Scaeurgus* sp. Degner, and in additional material obtained by the " Discovery " Expeditions (1925–1939).

(e) THE RADULA. The radula of a specimen from " Discovery " St. 1592 has been examined. It exhibits a symmetrical $^{A}3$–4 seriation of the cusps of the rhachidian, but there is some irregularity (perhaps to be expected in a young specimen). The first lateral tooth is narrow with a short pointed cusp, and the second lateral has a

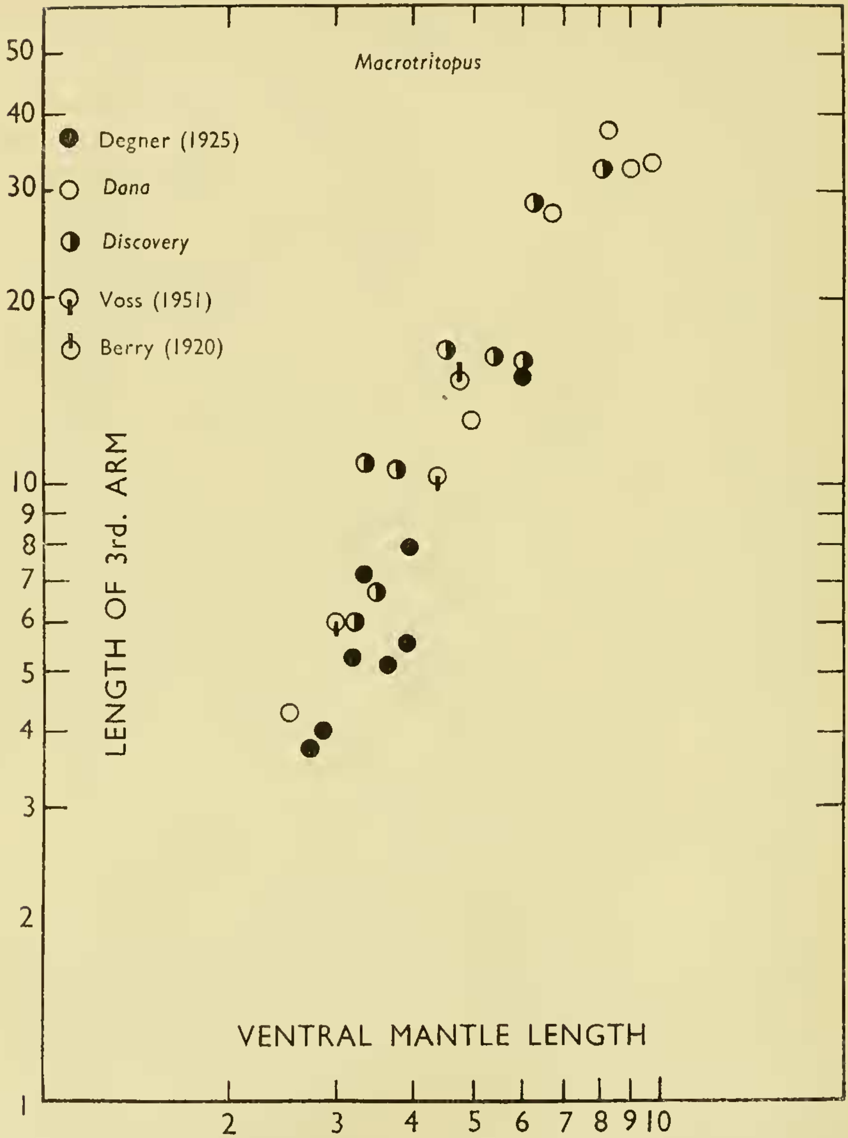


FIG. 13. Relationship of the third pair of arms to ventral mantle length in *Macrotritopus danae, M. kempi, M. scorpio, Scaeurgus* sp. Degner, and in additional material obtained by the " Discovery " Expeditions (1925–1939).

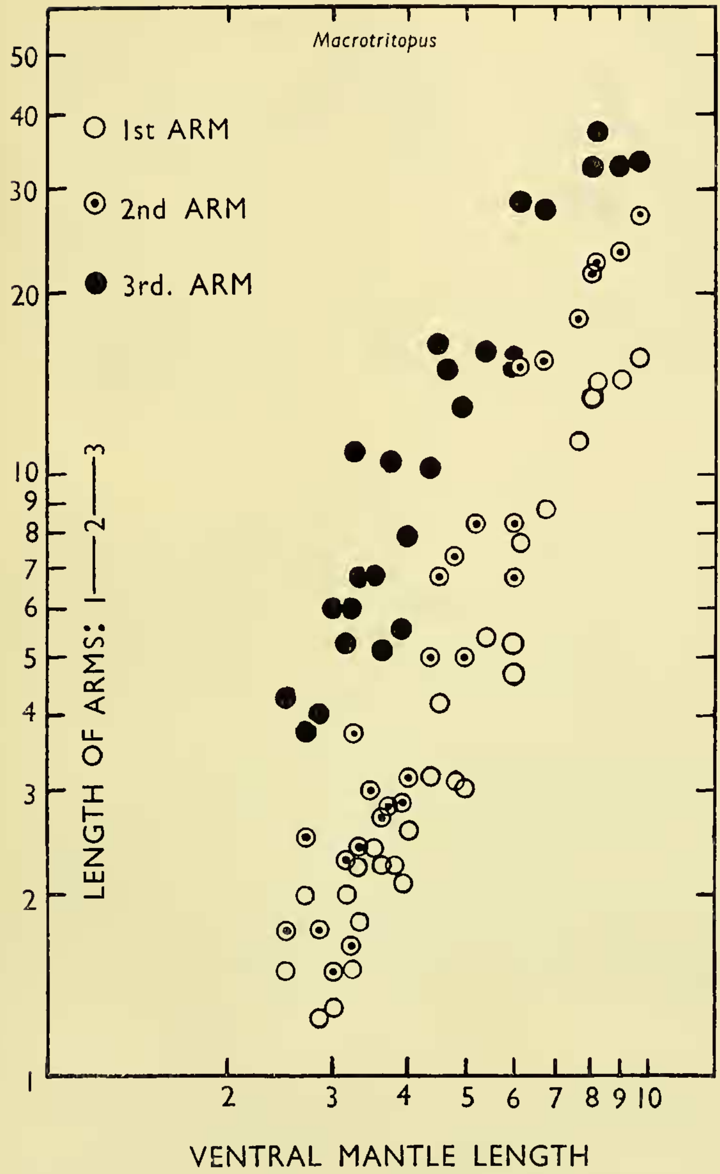


FIG. 14. Relationship of arms 1, 2 and 3 in relation to ventral mantle length in all the specimens examined.

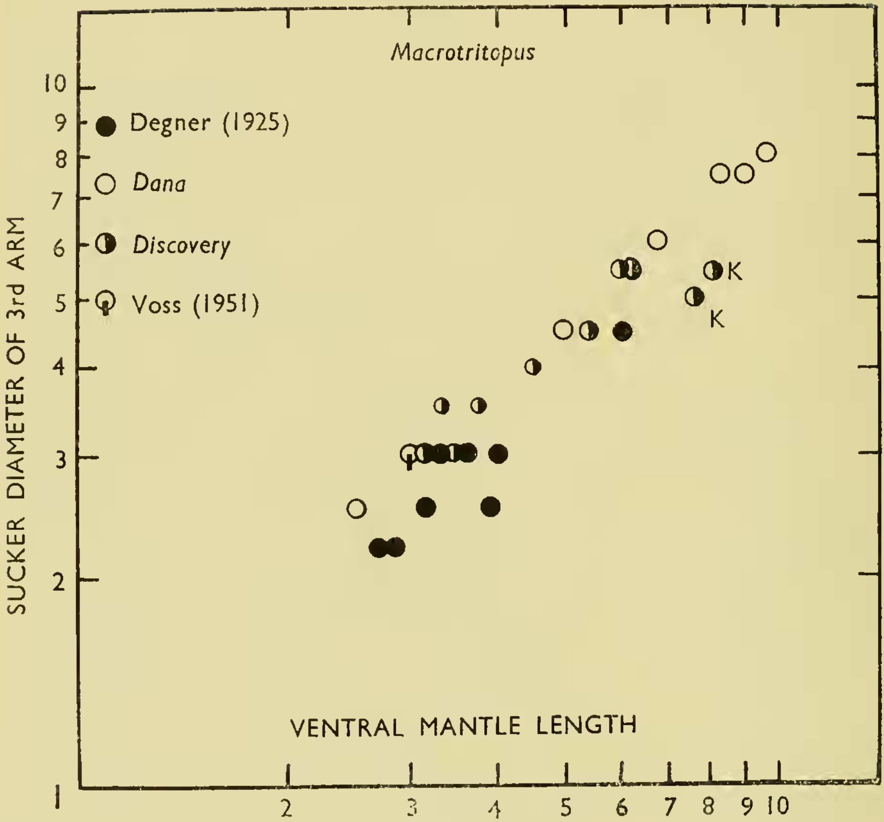


FIG. 15. Relationship of the sucker diameter of the third arm to ventral mantle length in *Macrotritopus danae*, *M. kempi*, *M. scorpio*, *Scaeurgus* sp. Degner, and in additional material obtained by the "Discovery" Expeditions (1925–1930). The letter *k* denotes the type material of *M. kempi*.

well formed endocone but no ectocone. The third lateral is distinctly long, slender and rather curved. The marginal plates are lozenge-shaped, a little broader than long.

The radula of the holotype of *Macrotritopus kempi* has also been examined and is very similar to the above, although details of the seriation of the cusps are difficult to interpret. Even though the preparation is a poor one, the cusps have a symmetrical arrangement and not an asymmetrical one as stated by Robson (1929, p. 312). The laterals are very similar to those of the specimen from " Discovery " St. 1592.

(f) Gill filaments. The number of gill filaments per demibranch has been noted in one specimen of each of the following : *Scaeurgus* sp. Degner, E. Mediterranean, 11 filaments ; *Macrotritopus kempi* Robson, West Africa, 11–12 filaments ; *Macrotritopus danae* Joubin & Robson, W. Mediterranean, at least 11 ; *Macrotritopus danae* Joubin & Robson, off Cuba, at least 11.

The third and fourth specimens listed above have deteriorated considerably in formalin, and the detailed structure of the gills, is not now very satisfactory for counting filaments.

All the evidence suggests that all the *Macrotritopus* larvae examined belong to a single wide-ranging species. I have not seen Verrill's *Macrotritopus* (*M. equivocus* Robson), but there appears to be no doubt about its identity with the other larvae ; it appears to be nothing more than a very large larva carried by water movements well beyond its normal range.

E. THE BREEDING SEASON

On the assumption that all the larvae belong to a single species it is possible to get some indication of the breeding period. We have to assume that once the eggs are laid (presumably at moderate depth) they take at least as long, if not longer, to hatch as in a littoral octopod. In *Octopus vulgaris* this is a period of 21–30 days, according to temperature, and it may be even longer in a deep-water species where sea temperature on its spawning grounds is likely to be lower.

In order to supplement the data obtained from the material studied, I have drawn on a list of occurrences given by Joubin (1937, p. 36) in addition to my own material. In the latter (Text fig. 16) ventral mantle length is taken as a criterion of size, while in the former overall length appears to be quoted (Text-fig. 17). As breeding may be largely controlled by temperature, the Mediterranean records have to be treated separately from those of the tropical Atlantic.

(a) The Mediterranean. In this warm temperate area we have records of larvae of all sizes but only for the months of August and September. It is true that during the Third " Dana " Expedition in 1921–22 the Mediterranean was visited only between 21st September and 4th October, 1921. The earlier expedition in the " Thor " (1908–1910) did, however, cover a much longer interval of time (14th December, 1908, to 21st February, 1909, and 26th June, 1910, to 7th September, 1910) but recorded larvae only in August.

If, as the meagre evidence suggests, larvae are common only in August and September, spawning must take place in June–July and possibly in August as well. By the end of September, when the largest larvae have been found, the majority are ready for settlement on the bottom, while a few late larvae may persist well into October. This is in agreement with Naef's statement that octopod larvae at Naples

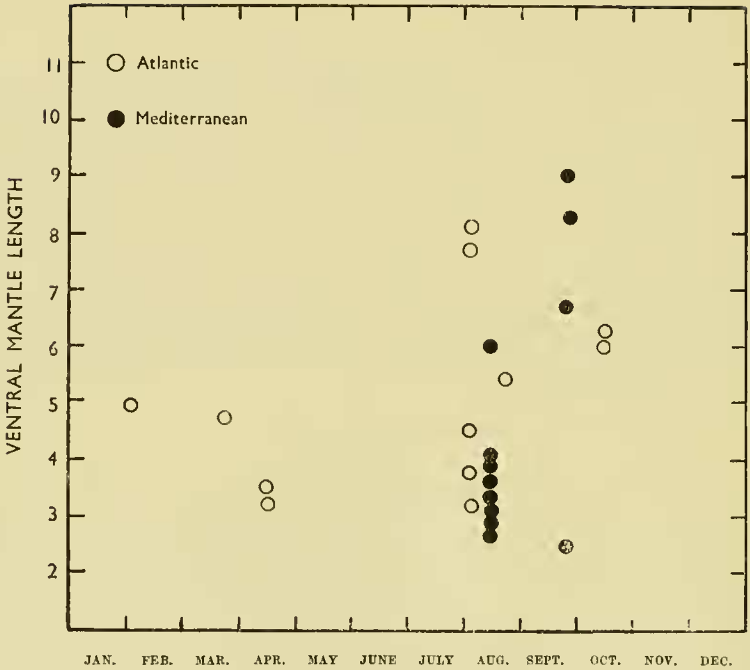


FIG. 16. Size (ventral mantle length) in relation to seasonal occurrence in the Atlantic and Mediterranean.

are more common in August and September than during other times of the year and suggests summer breeding.

(b) THE ATLANTIC. In the Atlantic only two larvae have been found to the north of 30° N. They were found at the following positions :

"Dana" St. 1152, 30° 17′ N., 20° 44′ W., S.W. of Madeira, 23.x.1921 ; 1 specimen of 18 mm.

"Dana" St. 1341, 33° 15′ N., 68° 20′ W., between Bermuda and the mainland, 14.v.1922 ; 1 specimen of 20 mm.

All the remainder were found in tropical or sub-tropical waters off West Africa and on the American coast, mainly off islands of the Greater and Lesser Antilles.

On the African coast the ships of the "Discovery" Committee took specimens in March, April, August and October during transit voyages to and from the Antarctic. There has, however, been no continuous sampling on this coast to give an accurate picture of seasonal distribution.

In the Central American region however the " Dana " was constantly taking plankton hauls between November, 1921, and May, 1922. There was no month in this period when larvae were not present. This implies that the breeding period was spread over the whole of this time, and if we take the records from West Africa and Florida into consideration, June is the only month for which larvae have not been recorded, and this apparent absence seems to be due to lack of observations.

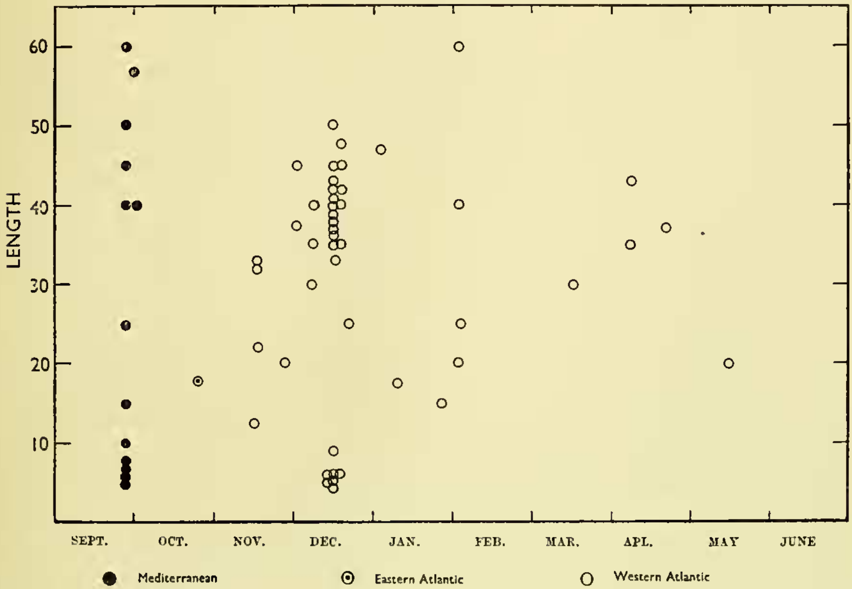


FIG. 17. Size (overall length) in relation to seasonal occurrence in the Atlantic and Mediterranean based on records of *Macrotritopus* spp. from the cruises of the " Dana " (1921–1922).

It is therefore clear that breeding may be noted in tropical and sub-tropical waters throughout the year. The greatest number of larvae (31) was taken in December, but the significance of this is not known. It may be that plankton hauls during this month were made in an area where there was concentration of breeding adults, or it might mean that this was the period of maximum breeding activity. If the latter it would imply maximum breeding in winter in the tropics—contrasting with summer breeding in the more temperate Mediterranean. In the Tropics, however, the factors which may exercise a big influence on temperature (which governs breeding) are local hydrographic conditions. For an animal which lives on the narrow coastal shelf (as off West Africa and the Antilles) local temperature conditions are bound to vary enormously according to movements of water masses, especially upwelling. Local breeding may therefore vary according to place and season.

V. THE SIGNIFICANCE OF THE *Macrotritopus* LARVA

The plankton life of the larvae of *Octopus vulgaris* (to judge from results hitherto unpublished) may have a duration of at least four weeks, and possibly eight or ten weeks under normal hydrographic conditions. For *Macrotritopus* it is reasonable to suppose a planktonic life of longer duration (perhaps for three to five months) on the basis that the larvae reach a much larger size. There is, however, another factor to be considered ; one of Degner's larvae from the comparatively shallow Gulf of Corinth was developing a hectocotylus at 6·0 mm. in ventral mantle length. To judge from evidence from all sources, including Naef's work in the Mediterranean, metamorphosis (here interpreted as the abandonment of a planktonic or pelagic phase) also means the beginning of sex differentiation and the development of gonads ; in the male the visible outward sign is the development of a hectocotylus. In the Gulf of Corinth the water is not very deep, and a larva ready to become benthic should find a suitable bottom at the right time, so that there would be no great delay in settlement. This implies that the ordinary *Macrotritopus* larva completes its planktonic phase at 6–7 mm. in ventral mantle length (allowance being made for the shrinkage of this material).

Other *Macrotritopus* larvae, however, reach a much bigger size without developing any sign of hectocotylus or of gonads. In *M. equivocus* the ventral mantle length is estimated to be 11 mm. ; in *M. kempi* and *M. danae* respectively it is 8·1 mm. and 9·75 mm. In view of the fact that I can find no other differences between these larvae and Degner's species, some other explanation must be sought for the non-appearance of signs of sexual differentiation or maturation, and I am inclined to interpret these large larvae as extended pelagic phases.

This phenomenon has been noticed before in marine invertebrates, but its significance does not seem to have been discussed in relation to distribution and dispersal. It is known from the work of Dr. Marie V. Lebour that in many molluscs a creeping-swimming stage of several days' duration is reached during metamorphosis, which, as suggested by Wilson (1937), may enable the larva to persist in a state whereby it can be swept away by currents to a more suitable substratum. From our present knowledge of the change to a benthic stage it is evident that species with a quick metamorphosis can delay settlement for several days, thus giving them a better chance of finding a suitable bottom.

When metamorphosis is gradual, settlement can be delayed for a long period, as has been demonstrated by Day & Wilson (1934) for the polychaete *Scolecolepsis fulginosa*. During this period of uncertainty the worm continues to grow beyond the 14-setiger stage at which these authors found metamorphosis to take place. In another polychaete, *Loimia medusa*, Wilson (1928) found that its planktonic existence ended when the larva had reached a length of about 6·0 mm. At this size the first pair of gills is beginning to divide, the second is only a rudiment and the third has not made its appearance. Still larger larvae were referred to the species by Monro (1930 and 1931) ; of these the largest example from "Discovery" St. 102 was 15 mm. long and had three pairs of well-developed gills. If we accept the view (as is most likely) that these larvae belong to the widely-distributed *Loimia medusa*, they can only be interpreted as an extended pelagic phase.*

Gurney (1942, pp. 71–75) gives details of several larvae of decapod crustacea which have been caught at sizes well above the known size for moulting into post-larvae. He was " reluctant to accept any theory of abnormality " for these giant larvae, and supposes that they had failed to metamorphose at the right time and continued to grow." He adds : " . . . in a situation like that of Bermuda, where abyssal depths are so close to the shore, it must be quite usual for larvae to find themselves over deep water at the time of metamorphosis."

Similarly when the distribution of *Macrotritopus* larvae is considered many of them were also taken fairly close to land, but in deep water off the edge of the continental shelf. At the places where they were taken (off West Africa and in the Antilles) the continental shelf is very narrow, so that the chances of larvae being swept over deep water are great. On the West coast of Africa, particularly, this seems to occur, and Knudsen (1950) attributes the high percentage of gastropods with very short planktonic or non-pelagic development on this coast to the influence of water movements in eliminating species with planktonic stages of long duration.

The *Macrotritopus* larva with its long third arms (which may be as useful as the squid's tentacles in catching food), its narrow squid-like profile and its curious colour pattern recalling that of the epipelagic larvae of the Cranchiidae, seems well adapted for a pelagic life. It may be that *Macrotritopus* specimens of above 6–7 mm. in ventral mantle length are larvae which have grown large in the plankton because they have not been able to find a suitable bottom (or a suitable bottom at the right depth) for metamorphosis. In other words delayed settlement has resulted in an extended pelagic phase which may be of considerable significance in dispersal. What is important is that it can travel immense distances in the plankton. The *M. equivocus* found off Cape Sable, Nova Scotia, had reached a mantle-sac length of 11 mm., and must have been transported for hundreds of miles by currents (probably from the Carribean or Florida) ; it was likely to be well out of the area in which it could survive as an adult. It may, however, be pertinent to draw attention to the rôle of the extended pelagic phase in maintaining uniformity in a wide-ranging species.

The remarkable similarity of populations of *Scaeurgus* from the Atlantic and Pacific was noted by Berry (1914, p. 306), who adds (*in litt.*, quoted by Voss, 1951) : " if it really is all one species, then there must be some special reason for lack of divergent speciation, and I can conceive no sensible explanation for this in a bottom form except for the possession of a planktonic larval stage of some duration."

G. THE IDENTITY OF *Macrotritopus* WITH *Scaeurgus*

When it became obvious that all the Altlantic *Macrotritopus* were referable to a single species, it was deemed possible to suggest a possible adult with which they

* Dr. Gunnar Thorson has kindly drawn my attention to Lemche's observations on the North Atlantic tectibranch *Diaphana minuta* Brown, which seem to suggest that the larva of this mollusc is able to delay metamorphosis when swept our over deep water (Thorson, 1946, p. 466 and Lemche, 1948, p. 9). In shallow water adults the embryonic shells are much smaller than those in specimens from depths exceeding 1,000 m. These larger embryonic shells are believed to indicate delayed settlement and resulting growth of the larval shell in specimens which have metamorphosed in deep water.

could be linked. When this paper was in early stages of preparation in 1950 there were four species with one of which they could possibly be linked, namely, *Octopus vulgaris*, *O. macropus*, *Scaeurgus unicirrhus* and *Pteroctopus tetracirrhus*.

The first, *O. vulgaris*, was the only species which had a known distribution corresponding most closely to that of the larvae (*Macrotritopus equivocus* being considered to have been carried well out of its normal distribution area). The details of the structure of the radula—asymmetrical in *O. vulgarus* and symmetrical in *Macrotritopus*—together with the occurrence of a normal larva of *vulgaris* in the same hauls as *M. kempi* (St. 276) were sufficient evidence that *O. vulgaris* could not be the adult.

The second, *O. macropus* Risso, has a similar but a more restricted distribution in the Mediterranean and both sides of the tropical Atlantic. This species, too, was ruled out because the details of the radula showed specific differences, and also because larvae of *O. macropus* were positively identified during the investigations.

Scaeurgus unicirrhus and *Pteroctopus tetracirrhus* were originally included in the list of possible adults, not because of any great similarity between the known distribution of the adults and that of *Macrotritopus*, but solely because each species had a sinistral hectocotylus. Degner's largest larva (specimen H) had a swelling at the tip of the third left arm, and on re-examination of the species I found it difficult to imagine its delicately rounded structure being the result of any malformation of the tip of the tentacle, and had to conclude that it was a true rudiment of a hectocotylus.

Evidence from distribution of the adults was not encouraging in 1950, especially as neither species had been found on the American side of the Atlantic and records outside the Mediterranean were very few. However, Voss (1951) gave the first records of *Scaeurgus* from the Western Atlantic (Florida), and Adam (1952) recorded *Pteroctopus* from West Africa. Full records of the two species outside the Mediterranean (where both are found) are given below:

Scaeurgus unicirrhus: Pacific Ocean; Hawaiian Islands (Berry, 1913 and 1914 as *patagiatus*); South of Kyushu (Sasaki, 1920 and 1929 as *patagiatus*); Indian Ocean; Saya de Malha (Robson, 1921); Atlantic Ocean, Florida (Voss, 1951).

Pteroctopus tetracirrhus: Atlantic Ocean; Cape Verde Islands (Fischer & Joubin, 1906 and 1907); Azores (Joubin, 1900); off the coast of Africa (Adam, 1952).

Scaeurgus appears from our present knowledge of distribution to have a much wider range than *Pteroctopus*; as both species live on moderately deep bottoms, it it not surprising that there are so few tropical records in view of the difficulties of operating trawls in areas where the bottom is covered with living or dead coral.

Both these species have a symmetrical arrangement of cusps on the rhachidian tooth of the radula as in *Macrotritopus*. A closer examination of the *Macrotritopus* radula shows that it agrees well with *Scaeurgus*, and differs from *Pteroctopus* in having a narrower first lateral tooth, a longer, more slender and more curved third lateral, and lozenge-shaped marginal plates. In *Pteroctopus* (see Adam, 1952, fig. 55) the marginal plates are wider and slightly curved in outline.

All the evidence suggests that *Macrotritopus* is the larval stage of *Scaeurgus unicirrhus*, and at present there is no indication that more than one species is involved. *Scaeurgus* has been found in the warm waters of all oceans, and its wide distribution (surprising in a bottom-dwelling animal) has clearly been achieved by this striking pelagic larva. The number of gill filaments per demibranch in *Scaeurgus* (11–14) is exceptionally high for a benthic octopod living at considerable depths near the edge of the continental shelf, but is probably related to the pelagic requirements of the larva.

H. CONCLUSION

All four Atlantic species of *Macrotritopus* have been demonstrated to belong to one species, also now linked with its adult, *Scaeurgus unicirrhus* (Delle Chiaje). *Macrotritopus* falls into the synonymy of *Scaeurgus*, and the position regarding the species is summarized as follows :

Scaeurgus unicirrhus (Delle Chiaje).
- *Octopus gracilis* Verrill, 1884, p. 236 *non* Eydoux & Souleyet, 1852, p. 13.
- *Macrotritopus gracilis*, Grimpe, 1922.
- *Macrotritopus equivocus* Robson, 1929*a*, p. 311.
- *Octopus* (*Macrotritopus*) *equivocus*, Robson, 1929*b*, p. 169.
- *Octopus* (*Macrotritopus*) *equivoca*, Joubin & Robson, 1929, p. 93 ; Joubin, 1937, p. 34.
- *Polypus scorpio* Berry, 1920, p. 299.
- *Octopus* (*Macrotritopus*) *scorpio*, Robson, 1929*b*, p. 169 ; Joubin & Robson, 1929, p. 93.
- *Macrotritopus kempi* Robson, 1929*a*, p. 311.
- *Octopus* (*Macrotritopus*) *kempi*, Robson, 1929*b*, p. 170.
- *Octopus* (*Macrotritopus*) *danae* Joubin & Robson, 1929, p. 87 ; Joubin, 1937, p. 33.
- *Macrotritopus* spp. Joubin, 1937, p. 36.
- *Scaeurgus* (Troschel sp. juv.) Degner, 1925, p. 79.

The great length of the third arm is a larval character only, for it is not found in the adult, in which the arms are subequal. The long third arm may have some special significance in larval life, serving perhaps for capturing food in the same way as the tentacles of the epipelagic squids. The high number of gill filaments, too, indicates an active larval existence which is in contrast with the low number found in octopods like *Bathypolypus* and *Bentheledone*, which are benthic deep-water octopods of the continental slope.

The records indicate that the *Macrotritopus* larva lives in the upper 200 metres. Most of the hauls from deeper water were made with open nets, so that positive conclusions cannot be reached from them, but the specimen taken by the " Discovery " with a closing net between 1,500 and 800 metres was at a surprising depth in a species which has all the appearance of being a surface form. Its occurrence at this depth suggests that it was seeking bottom preparatory to metamorphosis.

If we accept the occurrences of *Macrotritopus* larvae in the vicinity of land (or near the edge of the continental slope) as evidence of the existence of benthic adults nearby, *Scaeurgus* has a more general distribution in the warmer waters of the Atlantic than hitherto supposed. As already mentioned, the difficulties of trawling over coral in the tropics probably accounts for the scarcity of records of the adult.

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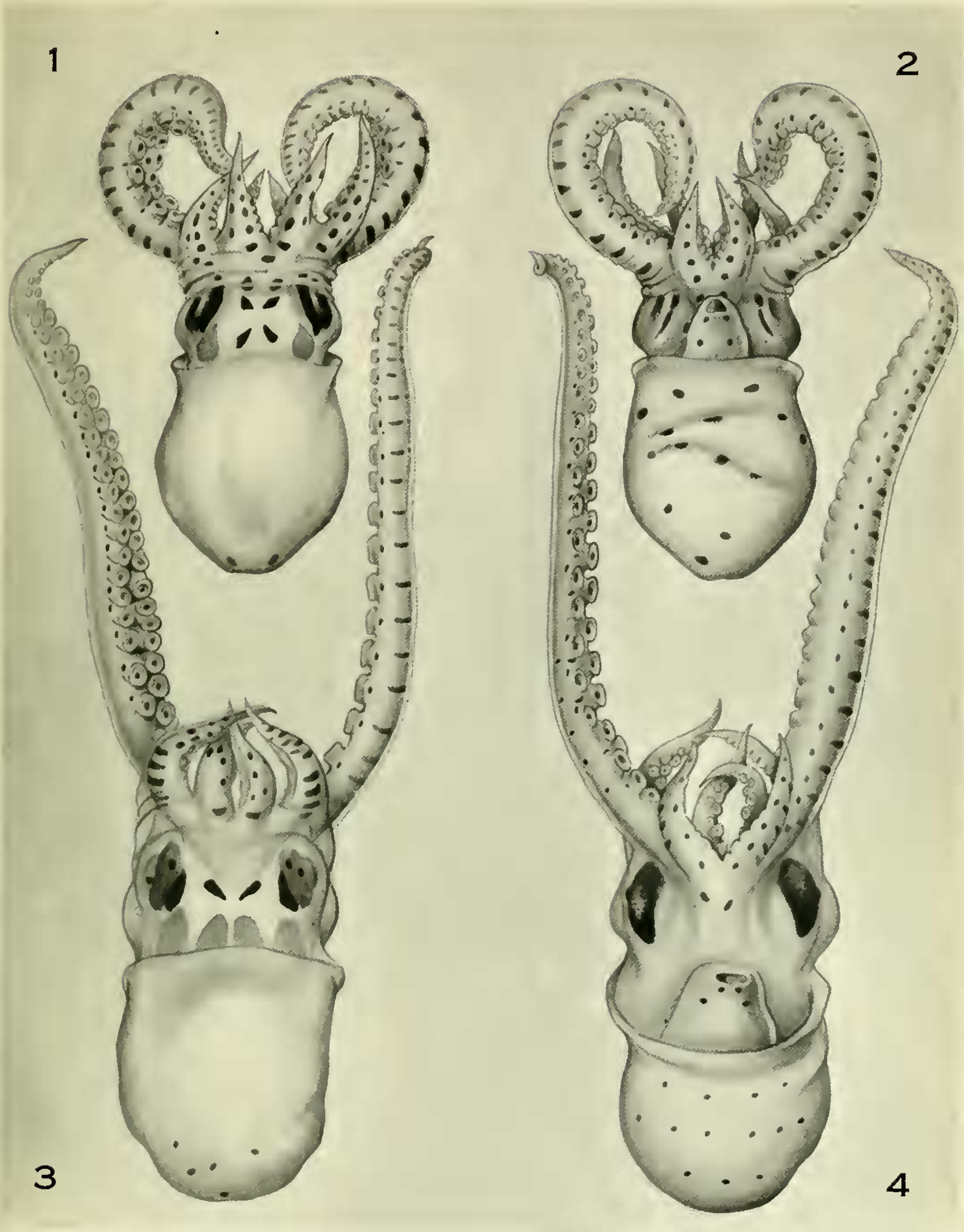
PLATE 3.

FIGS. 1 and 2. *Macrotritopus* larva of 3·45 mm. in ventral mantle length from "Discovery" St. 2646.

FIGS. 3 and 4. *Macrotritopus* larva of 3·75 mm. in ventral mantle length from "Discovery" St. 276. This specimen was taken in the same haul as Robson's syntypes of *M. kempi*.



MACROTRITOPUS LARVAE.